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Studies on African *Agama* V. On the origin of *Lacerta agama* Linnaeus, 1758 (Squamata: Agamidae)

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Abstract. Herein we present our strategy to preserve the nomenclatural stability of the widespread and common Afrotropical lizard *Agama agama* (Linnaeus, 1758). We recognized several proposed syntypes, belonging to a variety of species, i.e., *Agama agama*, *Agama atra* and *Tropidurus plica*. But we have shown that these specimens do not belong to the type material. However, if they were included in the type material the selection of the e.g. American syntype, *Tropidurus plica* – a tropidurine iguanid, as lectotype would result in taxonomic chaos, as *Agama agama* is an African species and includes in its synonymy the type species of the type genus of the family Agamidae. The illustrated types in SEBA (1734) are recognized by us as a variety of agamid lizards with a type locality encompassing the New and the Old World and not simply ‘America’, as given by LINNAEUS.

Morphologically, *Agama agama* is highly variable making it impossible to assign the syntype that agrees with the current concept of *Agama agama* to a geographic population, particularly as the only character, viz. the colour pattern, is no longer discernible in this specimen. This endangers the stability of the known subspecies of *Agama agama*. We therefore designate a neotype for *Lacerta agama* Linnaeus, 1758 herein.

Keywords. Nomenclature; taxonomy; neotype; Squamata; Agamidae; *Agama agama*; African rainbow lizard; type locality; Africa.

INTRODUCTION

The genus *Agama* Daudin, 1802 is one of the most widely distributed lizard genera within Africa, although the relationships between the species in the genus are still poorly known. *Agama* is a highly taxonomically complex genus and most of the taxa are very similar and highly variable in pholidosis and only identifiable by the nuptial colouration of males (McLACHLAN 1981, JACOBSEN 1992, WAGNER 2007). Therefore, it is often not possible to assign a single specimen with colouration lacking to a particular species or subspecies. This situation causes problems in the determination of type material to assess the validity of the different taxa. Thus, in many species and subspecies validity is doubtful (e.g., *Agama bocourti* Rochebrune, 1884; *Agama cornii* Scortecci, 1928; *A. picticauda* Peters, 1877; *A. congica* Peters, 1877). Past generic reviews have only been attempted for some

species groups (BOULENGER & POWER 1921, GRANDISON 1956, 1968) and most workers have considered it pointless to designate lecto- or neotypes to stabilize the nomenclature of the taxa. As an example, GRANDISON (1968) designated a lectotype of *Agama benueensis* Monard, 1951 (today recognized as a subspecies of *Agama doriae* Boulenger, 1885; see MOODY & BÖHME 1984), thereby stabilizing another *Agama* species because several individuals of the type series were identified as *A. paragama* Grandison, 1968. However, the situation has changed and several authors are now working on a broad scale phylogeny of the entire genus (WAGNER & LEACHÉ, own data). For this analysis it is essential to clarify the taxonomic status of *Agama agama* (Linnaeus, 1758) because many taxa are assigned to this species as synonyms or subspecies. Even in recent years several former subspecies of *A. agama* have



Fig. 1. Plate 107 published in *Thesaurus I* by SEBA (1734) showing three lizards described as '*Salamandra Americana*, posteriore parte *Lacertum referens*, *amphibia*; *mas*'.

14. *LACERTA* cauda tereti longa, pedibus pentadactylis, dorso antice denticulato, collo capiteque pone aculeato.

Salamandra americ. Lacertæ æmula altera. Seb. thes. I. p. 170. t. 107. f. 3. Salamandra amer. amphib. Seb. thes. I. p. 169. t. 107. f. 1, 2.

caput ovatum, squamis anteriora versus imbricatum, pone juxta aures aculeis inæqualibus spinofum, quod fingulare in hac specie. *Colum*

amphibia.

LACERTA cauda tereti longa, pedibus pentadactylis, dorso antice denticulato, collo capiteque pone aculeatis. *Amer. Acad.* 1. p. 288 *Syst. nat.* 36. n. 12.

Salamandra americana amphib. Seb. thes. I. p. 169. t. 107. f. 1, 2.

Salamandra amer. lacertæ æmula altera. Seb. thes. I. p. 170. t. 107. f. 3. Habitat in AMERICA.

Fig. 2. Description of '*Lacerta amphibia*' in the '*Amoenitates academicæ*' by LINNAEUS (1749, Vol. 1, p. 288).

been recognized as species. BÖHME et al. (2005) have elevated the *Agama lionotus* Boulenger, 1896 complex (*Agama lionotus lionotus* Boulenger, 1896, *Agama l. elongis* Lönnberg, 1922, *Agama l. dodomae* Loveridge, 1923, *Agama l. ufipae* Loveridge, 1932) leaving the true *Agama agama* to full species rank, with the following several nominal subspecies of its own: *Agama agama agama* Linnaeus, 1758; *Agama a. africana* Hallowell, 1844 (type locality: Liberia); *Agama a. boensis* Monard, 1940 (type locality: Madina Boé, Guinea-Bissau) and *Agama a. mucosoensis* Hellmich, 1957 (type locality: Mucoso near Dondo, Angola). *Agama a. savattieri* Rochebrune, 1884 [type localities: Casamance (Senegal?), Mélororée (Guinea?), Albréda (The Gambia), Bathurst (=Banjul, The Gambia)] has been synonymized with *A. agama africana* by GRANDISON (1968).

Even the status of these subspecies remains unclear and is dependent on the definition of *A. agama*. Therefore, it is essential to consult the original description by LINNAEUS (1758), the type specimens and previous descriptions of the species. The results of this search are herein presented.

1. PRE-LINNAEEN (BEFORE 1758) NAMES

'*Salamandra americana* Seba, 1734'

In his *Thesaurus* SEBA (1734) published a plate (thes. I, p. 170, t. 107) depicting three lizards (see fig. 1) which he described as '*Salamandra Americana, posteriore parte Lacertum referens, amphib; mas*'. The *Thesaurus* is published in two separate editions, one in French and Latin, the other one in Dutch and Latin. We herein recognize the Dutch edition because this would be the text that probably most accurately reflects SEBA's own language. In the Dutch part of the accompanying text he described the species shown in figure one of the plate as the

Fig. 3. '*Lacerta amphibia*' published in the '*Museum Adolphi Friderici*' (LINNAEUS 1754, p. 44) with the first mention in of the locality 'Habitat in America'.

'*West-Indische Salamander*' (= West Indian salamander), half salamander, half lizard. The specimens shown in figures two and three of the same plate (herein fig. 1) were also recognized as *Salamandra americana* but the figure captions were '*Wyfie van den voorgaanden Salamander*' (= the female of the above mentioned salamander) (figure two) and '*Ander soort van West-Indischen Salamander als de voregi*' (= another species as the previous one of the west Indian salamander) (figure three).

All the subsequent descriptions of the species refer to this plate and the text mentioned. The name '*Salamander americana*' is mentioned later by many authors (see below).

However, confusions among agamids, geckos and salamanders were common during the 18th and early 19th centuries. As an example, a gecko, today known as *Hemidactylus platyrus*, was described in an agamid genus as *Stellio platyrus* by SCHNEIDER (1792). In the same work SCHNEIDER (1792) also described *Stellio fimbriatus* from Madagascar, today known again as a member of the geckonid genus *Uroplatus*. Also *Trapelus savignyi* AUDOUIN, 1827, described in an agamid genus but in a gecko section of the text is today known as synonym of the gecko *Stenodactylus sthenodactylus* (Lichtenstein, 1823) (WAGNER & CROCHET 2009).

'*Lacerta amphibia* Linnaeus, 1749'

In the '*Amoenitates academicæ*', LINNAEUS' first important contributions as collected theses in seven volumes on systematics, he (LINNAEUS 1749, Vol. 1, p. 288; see fig. 2) described the lizard which was shown in SEBA (1734) as '*Lacerta canda tereti longa, pedibus pentadactylis, dorso antice denticulato, collo capiteque pone aculeato*' later known as '*Lacerta amphibia*' and synonymised the

Agama. 30. *L. cauda tereti longa, collo supra capiteque postice aculeato.*
Amen. acad. 1. p. 288.
Mus. Ad. Fr. T. p. 44.
Seb. mus. 1. t. 107. f. 1. 2. 3.
Habitat in America.
Color corporis pallidus. Abdomen minime striatum.

Fig. 4. Description of *Lacerta agama* in the nomenclaturally binding 10th edition of LINNAEUS 1758 (p. 207).

name '*Salamandra americana*'. In naming his species LINNAEUS referred to the plate published by SEBA (1734, plate 107; see fig. 1 herein) and obviously followed the suggestions of SEBA (1734), considering this species half salamander and half lizard. But LINNAEUS (1749) also referred to the differences between the specimens shown in the figures in SEBA (1734) as he synonymised figure three as *Salamandra americana* and figures one and two as *Salamandra americana amphibia*. Several years later, LINNAEUS (1754, p. 44) published his '*Museum Adolphi Friderici*'. Herein, he added a type locality as 'Habitat in America' and again he referred to two taxa (*Salamandra americana amphibia*, fig. 1 & 2; *Salamandra americana lacerate aemula*, fig. 3).

2. LINNAEUS (1758)

Lacerta agama Linnaeus, 1758

In the 10th and currently still binding edition of his guiding work, LINNAEUS (1758, p. 207) again re-named '*Lacerta amphibia*' to the currently valid *Lacerta agama* Linnaeus, 1758 (see fig. 4). In contrast to the descriptions before, he referred all the three images of plate 107 in SEBA (1734) to this monotypic species and mentioned again 'America' as type locality. In his description, LINNAEUS (1758) did not refer to other images or vouchers of a museum collection. Therefore, the individuals which are the basis of the illustrations in SEBA (1734) are the syntypes, because the 'International Code of Zoological Nomenclature' (ICZN 1999) does not recognize 'iconotypes' and no other types are mentioned. However, QUENSEL, director of the Swedish Academy of Science from 1799 to 1806, also mentioned three specimens (QUENSEL 1802, QUENSEL in ANDERSSON 1900) from the collection of the Museum Adolphi Friderici in Drottningholm and noted 'that they are identical with Linnaeus's *Lacerta amphibia*' (ANDERSSON 1900, p. 11). However, the use of 'identical' here only means identical to species not identical type specimens.

ANDERSSON (1900) examined these specimens and identified two as 'true *Agama colonorum* Daudin, 1802' and the last as '*Uraniscodon plica* Linnaeus, 1758'. A recent examination by us of the three specimens (Museum Adolphi Friderici: NRM 107, 108, 112; see fig. 5 herein) revealed that they represent three different valid species: *Agama* cf. *agama* (LINNAEUS, 1758), *Agama atra* Daudin, 1802 and *Tropidurus plica* (Linnaeus, 1758). But two of these specimens are without doubt not identical with the individuals illustrated in SEBA (1734). As it is obvious, the lizards shown in figures one and two clearly have segmented tails, which are not only lacking in the three museum vouchers, but also in the genus *Agama* in general. These segmented tails, which are arranged in whorls, are typical for the species of the genera *Acauthocercus* Fitzinger, 1843 and *Laudakia* Gray, 1845 (both Agamidae) occurring in Africa, Asia and Europe. Only the specimen of figure three shows a tail typical for *Agama*, but also for the South American genus *Tropidurus*. These differences were also recognized by DUMÉRIL & BIBRON (1837) who referred the specimens shown in figures one and two of plate 107 in SEBA (1734) to *Stellio vulgaris* Sonnini & Latreille, 1802 (today known as *Laudakia stellio vulgaris*) and erroneously synonymised *Lacerta amphibia* with *Agama colonorum*, as they only referred figure three to *Agama colonorum*.

However, it is obvious by comparing the NRM specimens with the remaining image in SEBA (1734) that it is not identical with one of the specimens. The *atra* specimen has a very different colouration, whereas the *plica* one has the mouth closed, but similar in scalations to the figured specimen. The cf. *agama* specimen is not identical in head scalation and proportion.

Consequently, the NRM specimens are not identical with the lizards shown in SEBA (1734) and are not type specimens of *Lacerta agama* Linnaeus, 1758. As a nomenclatural stabilization of this name is indispensable for further research, a neotype is designated by us (see below).

However, even if e.g. the most similar NRM voucher (the *T. plica*-specimen) to the remaining image were the name-bearing type of *Lacerta agama*, it would require suppression because it would destabilise two well known species, two genera and two families.

Thus *Tropidurus plica* (as currently known) would become *Lacerta agama*. However, *Agama colonorum*, a synonym of *Lacerta agama* today known as *Agama agama*, is also the type species of the genus *Agama*. Therefore, *Tropidurus plica* and closely related taxa like *T. humaria* and *T. umbra* would become members of the genus *Agama*.

Further, the genus *Agama* is the type genus of the lizard family Agamidae. This would mean that these Old World lizards would lose their name to a New World genus, which would cause a taxonomic chaos and is therefore obviously unacceptable.

According to article 75.6 of the ICZN this approach should not be taken into consideration because it endangers the stability of the well known species *T. plica*, the genus *Agama* and the family Agamidae.

Remarks on the identity of the NRM specimens

As shown above, two of the specimens are not identical with *Agama agama* as they are identified as *A. atra* and *Tropidurus plica*. The remaining voucher (fig. 5c) is a true *Agama* species, and probably *Agama agama* itself. It is obvious from figure 5c that the specimen is in good con-

dition but completely lacking colouration. As previously noted, species of the genus *Agama*, and especially *Agama agama*, are characterized by a high variability of scale counts (BOULENGER & POWER 1921, THIJS VAN DEN AU-DENAERDE 1963, GRANDISON 1968, MOODY & BÖHME 1984, BÖHME et al. 2005) and therefore nearly all taxa are determined by aspects of colouration of adult males (MCLACHLAN 1981, JACOBSEN 1992, WAGNER 2007). Thus, it is not possible to assign this voucher to a specific *Agama agama* population or subspecies and even not clearly to *Agama agama* itself.

Remarks on the erroneous type locality 'America' & the nomen *Agama*

Today it is obvious that the type locality 'in America' is erroneous and does not correspond with the actual distribution of the species, genus and family. Surprisingly, *Agama colonorum* Daudin, 1802, the first available synonym of *Agama agama*, was also described from 'l'Amerique méridionale', 'Cuba' and 'Jamaïque'. DAUDIN (1802) suggested this name for *Lacerta agama* Linnaeus, 1758 and mentioned several names (e.g. *Lacerta agama*; *Ignara cordylina* Laurenti, 1768; '*Salamandra americana* Seba, 1734'; *Lacertus major* Sloane; Guana lizard Brown; Blue lizard Edwards; L'agame Daubenton; L'agame ou caméléon de Mexique Stedman) as synonyms. Additionally, DAUDIN (1802) also mentioned aspects of the linguistic usage of the name 'agama' and mentioned that the name is used for a variety of different lizard species in South America. However, the source of the name 'agama' is from the Ewe language of the Kwa group, spoken in Togo, Benin and Ghana (BAUMANN 1936, WESTERMANN 1954). DUMÉRIL & BIBRON (1837) were the first who recognized that the type locality is in error and mentioned a distribution of the species 'sur la côte de Guinée et au Sénégal' (= at the coast of Guinea and in Senegal).

However, the consideration of the type locality as 'in error', the simplest solution, does not solve the problem. According to article 76 of the code, the 'type locality of a nominal species-group taxon is the geographical place of capture, collection or observation of the name-bearing type; if there are syntypes and no lectotype has been designated, the type locality encompasses the localities of all of them'. As the syntypes are not available, the type locality can only be concluded from the identified lizard genera shown on the plate in SEBA (1734).

MERTENS (1938) also recognized the problem and restricted it to 'Cameroon', but without the designation of a lecto- or neotype. According to article 76 of the code, MERTENS' (1938) restriction was invalid and the type locality thus still not clarified.



Fig. 5. Formerly supposed syntypes of *Lacerta agama* Linnaeus, 1758 in the Museum Adolphii Friderici (NRM 107, 108, 112). A= *Tropidurus plica* (Linnaeus, 1758); B= *Agama atra* Daudin, 1802; C= *Agama cf. agama* (Linnaeus, 1758).

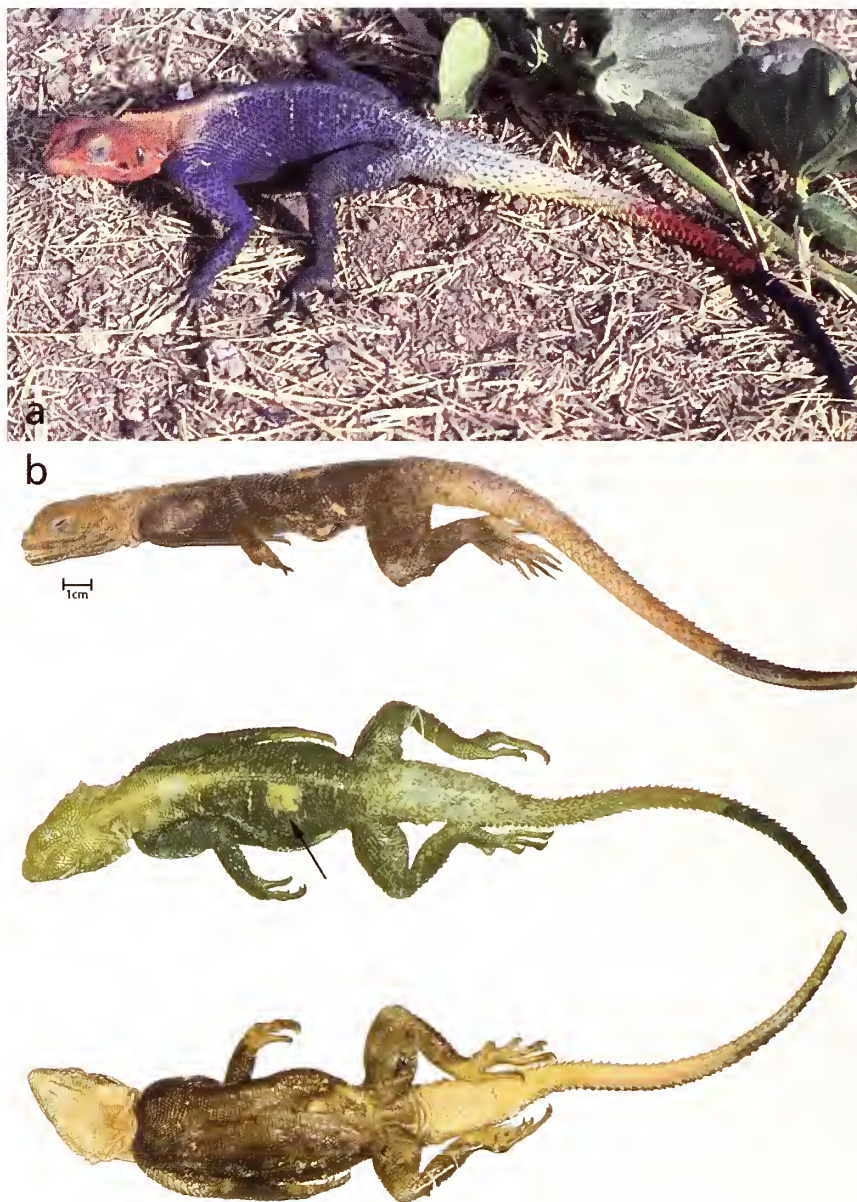


Fig. 6a. Neotype of *Lacerta agama* Linnaeus, 1758 (ZFMK 15222): a = image of the living neotype; b = complete lateral, dorsal (arrow indicates the place of scales used for SEM images, see fig. 6c), ventral body views.



Fig. 6b. Neotype of *Lacerta agama* Linnaeus, 1758 (ZFMK 15222): details of head scalation.

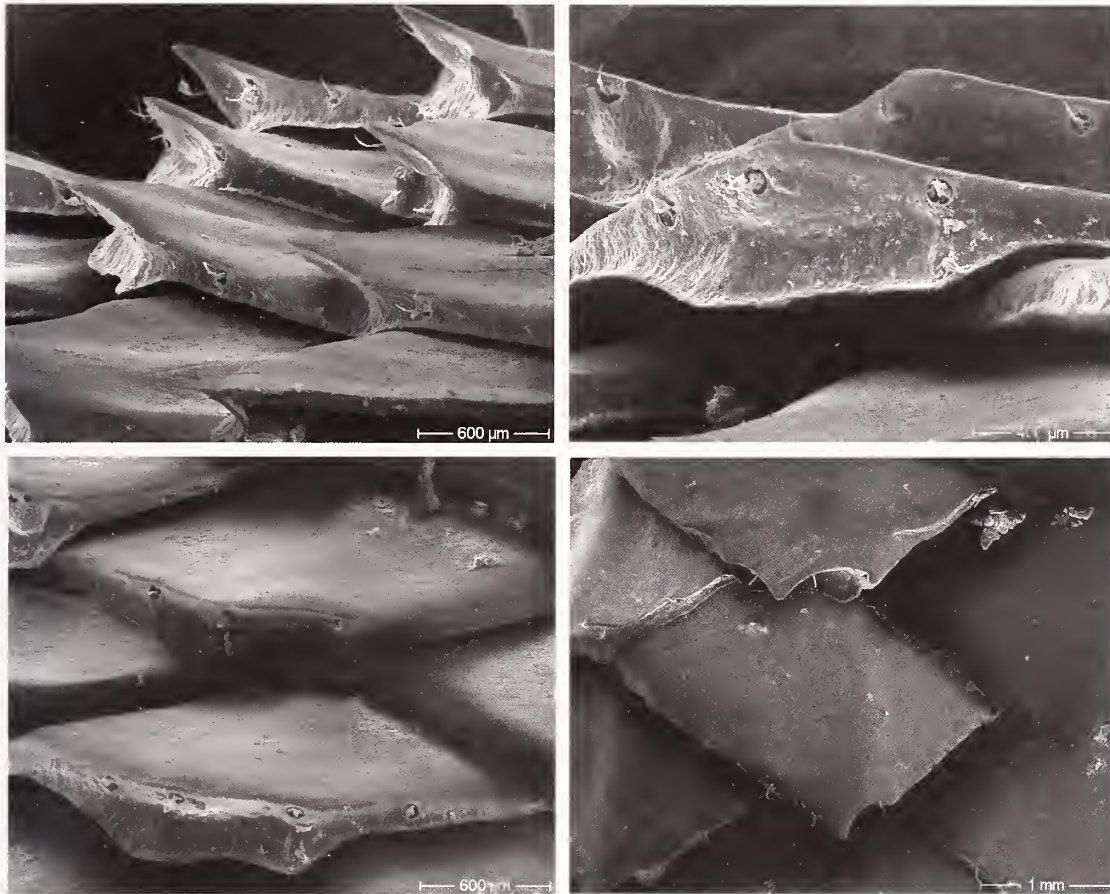


Fig. 6c. Neotype of *Lacerta agama* Linnaeus, 1758 (ZFMK 15222): SEM images of dorsal scales. Location of the scales is indicated by an arrow in fig. 6a.

Description of *Lacerta agama* Linnaeus, 1758

Agama agama (Linnaeus, 1758)

- 1734 *Salamandra americana* Seba, Naturalium Thesauri, thes. 1, Tome 1, Pl. 107, fig. 1–3.
- 1749 *Lacerta amphibia* Linnaeus, Amoenitates academicae, vol. 1: 288.
- 1754 *Lacerta amphibia* Linnaeus, Museum Adolphi Friederici: 44.
- 1758 *Lacerta agama* Linnaeus, Syst. Nat., Ed. 10, 1: 207.
- 1802 *Agama colonorum* Daudin, Hist. Nat. gén. Part. Rept. 3: 358.
- 1831 *Agama occipitalis* Gray, in Griffith, Animal Kingdom Cuvier, 9 Synops. Spec.: 56.
- 1844 *Tropidolepis africanus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia 1844: 171. Type locality: Liberia.
- 1877 *Agama colonorum* var. *congica* Peters, M. Ber. K. preuß. Akad. Wiss. Berlin. 1877: 612.
- 1877 *Agama picticauda* Peters, M. Ber. K. preuß. Akad. Wiss. Berlin. 1877: 612.

- 1884 *Agama agama savattieri* Rochebrune, (synonym of *A. a. africana* fide Grandison 1968) Faune Sénégal, Rept.: 89.
- 1896 *Agama smithii* Boulenger, (fide Largen & Spawls 2006), Proc. zool. Soc. London 1896: 213.
- 1940 *Agama boensis* Monard, Arq. Mus. Bocage, Lisboa 11: 155. Type locality: Madina Boé, Guinea.
- 1957 *Agama agama mucosoensis* Hellmich, Veröff. Zool. Staatsamml. München 5: 44. Type locality: Dondo, Angola.

Neotype. ZFMK 15222: Mokolo, Margui-Wandala Province, northern Cameroon, leg. W. BÖHME & W. HARTWIG, 14.II.1974 (figs 6a–c).

Diagnosis. A large species of the genus. The nuptial male of *Agama agama* is characterized by a yellow head, a red throat and a tri-coloured (yellow, red and black) tail. The subordinate males, females, and adolescents possess an olive-green head and an olive-green to brown body with yellow dots, ocelli and stripes.

Description of the neotype of *Lacerta agama* Linnaeus, 1758

Adult male, measuring 290.11 mm in length (snout-vent length 128.93 mm, tail 161.18 mm, head length 33.49 mm, head width 23.61 mm, head height 14.07 mm).

Nostril slightly above the canthus rostralis, pierced in the middle of a large vaulted nasal scale, directed obliquely posterodorsally. Between the nostrils is a longitudinal, finely keeled shield, followed by finely keeled to smooth, regularly arranged scales in the interorbital region and on the remaining upper side of head. Supraocular scales are smooth. Parietal shield more or less pentagonal, parietal organ slightly visible. Nine supralabial scales on the left, eight on the right side, nine infralabial scales on both sides. The scales originating from both sides of the parietal midline have their imbrications anteriorly directed; the keels in the upper temporal region have their mucrones at the anterior margins. Ear-opening large, about the same size as the eye; tympanum visible; anterior margin being composed of spiny, mucronate scales. Four spiny tufts on the left side and five on the right, one before the ear opening, one above, one to two below and one to two behind. Nuchal crest low, consisting of 13 weakly differentiated lanceolate scales. Gular scales flat, juxtaposed and becoming smaller towards the gular fold. Dorsal scales keeled, becoming larger from neck and tail to the middle of the body; in 58 scale rows around midbody. Scales on tail arranged in weakly but nonetheless distinctly differentiated whorls that consist of three scale rings each, dorsally strongly, ventrally weakly keeled to smooth. Ventral scales smooth, slightly to strongly imbricate at their posterior margin; in 80 rows between throat and vent. One row of 10 preanal pores. Scales on forelimb with strongly keeled scales, on the upper arm twice as large as the dorsals, becoming smaller towards the underside and the manus. 3rd and 4th finger longest, 4th slightly longer, digital length decreasing 2–5–1, subdigital lamellae keeled. Hindlimbs also covered by distinctly keeled scales, on the upper thighs twice as large as the dorsals, becoming larger towards the lower thighs and smaller towards the underside.

Colouration in life. Head and nape reddish, limbs and body blue, base of tail white, followed by red and then black.

Remarks. The rank of the two subspecies *boensis* and *mucosoensis* is questionable. GRANDISON (1968) mentioned *boensis* as a large-scaled *Agama* species and therefore some vouchers from Guinea could be identical with that taxon and in this consequence *boensis* should be elevated to species rank (WAGNER & INEICH unpubl. data). *Agama a. mucosoensis*, with its striking blue and yellow

colouration is as different to *A. a. agama* as *A. planiceps*, *A. lionotus* and many more well diagnosed species of the genus. Therefore it is very doubtful that *mucosoensis* is a subspecies of *agama*.

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